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Oecologia

DOI:
10.1007/s00442-019-04496-9

Published: 01/10/2019

Peer reviewed version

Ecosystem Ecology – *Original Research*

Foraging consistency of coral reef fishes across environmental gradients in the central Pacific

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Author Contributions: BJZ and SAS conceived and designed the project. BJZ and SAS led logistical efforts for research expeditions. BJZ, SLH, and SAS carried out field collections. BJZ and EGC led dissection and sample processing efforts. BJZ, MDF, RHM, and LSK performed stable isotope analyses. BJZ, GJW, YE, and SAS performed statistical analyses. BJZ, GJW, and SAS wrote the manuscript; other authors provided insights and editorial advice throughout the development and completion of the manuscript.

Abstract –

We take advantage of a natural gradient of human exploitation and oceanic primary production across five central Pacific coral reefs to examine foraging patterns in common coral reef fishes. Using stomach content and stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses we examined consistency across islands in estimated foraging patterns. Surprisingly, species within the piscivore-invertivore group exhibited the clearest pattern of foraging consistency across all five islands despite there being a considerable difference in mean body mass (14g-1.4kg) and prey size (0.03-3.8g). In contrast, the diets and isotopic values of the grazer-detritivores varied considerably and exhibited no consistent patterns across islands. When examining foraging patterns across environmental contexts, we found that $\delta^{15}N$ values of species of piscivore-invertivore and planktivore closely tracked gradients in oceanic primary production; again, no comparable patterns existed for the grazer-detritivores. The inter-island consistency in foraging patterns within the species of piscivore-invertivore and planktivore and the lack of consistency among species of grazer-detritivore suggests a linkage to different sources of primary production among reef fish functional groups. Our findings suggest that piscivore-invertivores and planktivores are likely linked to well-mixed and isotopically constrained allochthonous oceanic primary production while grazer-detritivores are likely linked to sources of benthic primary production and autochthonous recycling. Further, our findings suggest that species of piscivore-invertivore, independent of body size, converge toward consuming low trophic level prey, with a hypothesized result of reducing the number of steps between trophic levels and increasing the trophic efficiency at a community level.

Keywords: *Fishes; Foraging; Trophic; Stomach contents; Isotopes; Primary production*

Introduction – The high diversity of fishes living on coral reefs is a distinguishing feature of this community, provoking considerations of how so many species can coexist in a limited area. Foraging specializations appear to be one axis along which reef fishes partition niche space (Adam et al. 2015). The first-order foraging constraints linked to body and gape size are represented broadly among reef fishes, with species ranging 7-8 orders of magnitude in mean adult mass (most species between 0.1g and 100kg) with a putatively wide range of associated specialties of prey size ranges across fish size classes. Notable adaptations that introduce specialized foraging opportunities include extreme morphological characteristics (e.g., elongated mouths within the *Forcipiger*, fused teeth of the scarinae) and behavioral peculiarities (e.g., tight microhabitat specialization within *Paracirrhites*) (DeMartini 1996; Wainwright and Bellwood 2002). Detailed dietary assessments have elucidated additional forms of dietary specialization among taxa that have seemingly very similar autecologies, for example as observed from compound-specific stable isotope diet reconstructions among two species of cohabitating *Lutjanus* with non-overlapping diets (McMahon et al. 2016).

Despite an often-astounding degree of morphological specialization (Motta 1988; Wainwright and Bellwood 2002), evidence suggests that some species of coral reef fish can exhibit a broad flexibility in diet, and generalist or omnivorous feeding can be found ubiquitously across trophic levels (Bellwood et al. 2006; Crossman et al. 2005). Some such foraging generalizations are ontogenetic within species, with juveniles exploiting distinct food resources from adults within the same environment (Lukoschek and McCormick 2001; St John 1999). Even within taxa of similar age classes, some mid-to-low-trophic level consumers (operationally defined as ‘carnivores’ or ‘herbivores’) may feed opportunistically or incidentally across traditional trophic boundaries. For instance, putative herbivore species often consume

69 micro-invertebrates hidden within algal turfs or coralline algae (Crossman et al. 2005; Kramer et
70 al. 2013). Further, some large-bodied top-predatory fishes subsidize a predominantly piscivorous
71 diet with invertebrate prey and forage across multiple habitats serving as important couplers of
72 discrete energetic pathways (Matich et al. 2011; McCauley et al. 2012). Recent research has
73 suggested that some species of mesopredatory fishes will shift prey in response to dramatic
74 changes in reef environmental context (e.g., bleaching; (Hempson et al. 2017)). It remains an
75 open question whether such generalized foraging patterns themselves are characteristic, with
76 species (or specific age classes of species) consistently consuming a distinct combination of prey
77 relative to heterospecifics.
78 Despite our growing understanding of the diverse feeding ecologies observed among reef
79 fishes, we have a limited understanding of how the diets of reef fishes within putative trophic
80 groupings respond across anthropogenic and environmental gradients. Most reef fisheries target
81 species across larger size classes and multiple trophic levels, the consequences of which alters
82 food web structure even at moderate levels of extraction (Graham et al. 2017; Zgliczynski and
83 Sandin 2017). The influence of shifted food web structure, with potentially compounding
84 behavioral shifts (Dill et al. 2003), on species-specific foraging patterns is less-well understood.
85 Superimposed over these predator-prey relationships are abiotic forcings including ocean
86 currents, internal waves, and eddy-diffusion that deliver pelagic energy and nutrient subsidies in
87 the form of dissolved nutrients and allochthonous plankton to coastal marine communities (Gove
88 et al. 2016; Williams et al. 2018). While oceanographic context certainly influences the
89 composition of reef fish assemblages, much less is known about these influences on species-
90 specific foraging patterns and food web structure.

91 The diversity of coral reefs, while providing an invaluable opportunity for studying
92 foraging specialization, also provides significant challenges in quantifying feeding patterns. The
93 potential prey field is highly diverse, including micro- and macro-algae, benthic invertebrates,
94 and other fishes (Plaisance et al. 2009; Stella et al. 2010). Further, the relative trophic structure
95 of the prey field can be similarly diverse with prey species consuming food resources stemming
96 from distinct basal sources including oceanic production, benthic production, and myriad
97 microbial shunts of production and remineralization (Gove et al. 2016; Silveira et al. 2017;
98 Somera et al. 2016). As such, in order to investigate the realized foraging patterns of reef fish
99 across environments, there can be extreme data demands. If one were to employ stomach
100 contents analyses to compare diets of fishes across environments, the guts of very many
101 individuals per environment would need to be sampled. Because there are so many potential prey
102 items and species, and because stomach contents represent only a brief window of foraging time
103 for the sampled individual (determined by species-specific gut transit times), 100s to 1000s of
104 individual guts must be sampled to gain a precise estimate of site-specific foraging patterns for a
105 particular species (Deb 1997; Hyslop 1980).
106 Stable isotope analysis is a complementary approach used to infer foraging patterns
107 (Bearhop et al. 2004). When the potential diet items are known and carry relatively distinct
108 isotopic signatures, mixing models can be used to estimate the proportional representation of
109 each to a sample individual's diet (McCauley et al. 2012; McMahon et al. 2016). However,
110 among many coral reef fishes the potential diet items are many and some fishes are known to
111 forage across multiple sub-habitats (e.g., fishes moving from reef flats to forereefs). As such, a
112 taxonomically precise estimate of foraging patterns of a coral reef fish would require extensive
113 stable isotopic sampling of myriad potential prey sources (perhaps from multiple sub-habitats).

Most successful applications of stable isotopic analysis among coral reef fishes have focused on the testing of hypotheses of broad habitat use (McCauley et al. 2012; Wyatt et al. 2012), focal investigations of target taxa from individual locations (Hempson et al. 2017; McMahon et al. 2016), and human induced changes to food web-structure (Layman et al. 2007).

While there are limitations linked to the use of stomach contents analysis (SCA) and stable isotope analysis (SIA) to resolve the diets of individual species, these approaches provide value for exploring hypotheses of relative foraging patterns of species across locations. These tools can provide a snapshot of context-specific foraging habits, i.e., proxies of foraging patterns (SCA and SIA) collected factorially across multiple species and multiple environments. A robust null model of foraging consistency across environments would be the expectation that relative differences in SCA or SIA data between species in a single environment are maintained consistently among the multiple environments. This null model would be supported if realized foraging patterns of species are little affected by environmental context, and is consistent with views of species-specific foraging specialization. In contrast, a null model of consistent relative differences in SCA or SIA data can be rejected due to multiple mechanisms. Biologically, if the foraging of individual species varies as a matter of environmental context, we will expect relative differences among species to vary – SCA will reveal different food items by context and SIA will reveal non-consistent inter-species differences. Notably, and especially for SIA, vagaries of isotopic signatures of potential prey across environmental contexts can also lead to rejection of this null model. If basal isotopic signatures vary in a non-consistent manner across geography and change one species' prey differently than another, it is possible to observe variable inter-species relative isotopic positions even without changes in foraging patterns. In sum, rejection of the null of consistent relative differences of species among environments can

occur via multiple mechanisms, both biological and operational; failure to find strong evidence rejecting the null however is most consistent with evidence of among-species foraging consistency across environments.

In this study, we explore how the relative foraging habits of common coral reef fishes are affected by local environmental context, namely the forereef habitats of five islands in the Line Islands Archipelago (central Pacific). The islands span a gradient in oceanic primary production, in the form of allochthonous nutrient and planktonic delivery, and a distinction of fisheries exploitation including three unfished and two moderately exploited reefs. We target eight species of coral reef fishes that are among the most abundant species in the region, representing three trophic groups (piscivore-invertivore, planktivore, and grazer-detritivore). We test hypotheses of foraging consistency across islands, determining which, if any, species groups show relative invariability of diets across this well-described gradient of oceanic primary production and fishing pressure.

Methods –

Study Sites

The northern Line Islands (NLI) are located more than 1500 km south of the Hawaiian Archipelago in the central Pacific (Fig. 1). Islands range from unfished reefs representative of intact ecosystems, through to fished reefs with significantly reduced predator biomass (DeMartini et al. 2008; Sandin et al. 2008). Fish assemblages surrounding the unfished islands are characterized by an abundance of large-bodied species including the prevalence of top-level predators that often contribute over 50% of the total fish biomass (DeMartini et al. 2008; Sandin et al. 2008). In contrast, inhabited islands support modest nearshore fisheries and fish assemblages characterized by lower overall biomass and a disproportionate reduction in the

large-bodied predatory species (Zgliczynski and Sandin 2017). Further, the NLI are exposed to a latitudinal gradient in oceanic primary production, with estimates of production nearly doubling across the island chain (Fig. 1). Regional current patterns and localized upwelling result in greater nutrient availability and enhanced planktonic production at islands with increasing proximity to the equator (Gove et al. 2016).

Fish Sampling

Sampling was conducted across five of the NLI (from north to south: Kingman, Palmyra, Teraina, Tabuaeran, and Jarvis; Fig. 1) during a ship-based expedition between Oct - Nov 2010. At each island, we collected samples of eight coral reef fish species across a range of body sizes and functional trophic groups. We used the results of previous survey efforts as a guide to identify species that represent the largest contributors to abundance and biomass of the fish assemblage (DeMartini et al. 2008; Sandin et al. 2008) (Table 1). Targeted species included (with putative functional trophic group): *Lutjanus bohar* (piscivore-invertivore), *Cephalopholis urodeta* (piscivore-invertivore), *Paracirrhites arcatus* (piscivore-invertivore), *Pseudanthias bartlettorum* (planktivore), *Chromis margaritifer* (planktivore), *Stegastes aureus* (grazer-detritivore), *Acanthurus nigricans* (grazer-detritivore), and *Ctenochaetus marginatus* (grazer-detritivore). Reviews of the general feeding ecology of these species can be found in natural historical reports and field guides (Randall 2005). Together these eight species accounted for 30% and 23% of the total fish abundance and biomass from coral reefs in the region (Table 1).

A target number of 50 individuals across a range of body sizes were collected using hand nets, pole spears, and hook-and-line to obtain representative samples for each species-island combination. To minimize the effects of ontogenetic dietary variation for this study, we constrained the size classes of samples for each species-island combination to the regional mean

183 standard length (SL) based on collection efforts across islands (Table 1). In a few instances,
184 samples were collected during previous research campaigns, and to minimize impacts to coral
185 reef fish communities, we supplemented collecting efforts with these samples (Ruttenberg et al.
186 2011; Wood et al. 2014). We recognize that using samples from different years may introduce
187 potential dietary variability across years, however, samples collected during previous expeditions
188 represented only a small proportion (10%) of the total number of samples included in this study
189 (Table 1). Further, efforts were made to minimize the effects of dietary variation across all
190 sampling campaigns by collecting specimens along leeward forereef habitats (the reef slope
191 habitat exposed to the open ocean) at depths between 8-15 m. Therefore, the effects of potential
192 dietary variation across sampling campaigns are likely to be minimal.

193 *Assessment of Dietary Consistency*

194 To evaluate foraging consistency of focal species across islands we used a combination of
195 stomach content and stable isotope analyses. Traditional stomach content analysis was used to
196 quantify dietary composition and the relative contribution of prey items to the diet of each
197 species (Hyslop 1980). Efforts were made to select 20 stomach contents samples from each
198 species-island combination around the regional mean SL for each species whenever possible
199 (Table 1). In some cases, the stomachs of fishes were empty and additional specimens were
200 dissected in an effort to include 20 individuals for each species island combination in the diet
201 assessment. Items within the stomach were removed, weighed, and assigned to the finest
202 taxonomic resolution feasible. With all diet constituents identified, a two-tiered hierarchy of diet
203 categories was constructed (Online Resources 2-4). Diet category subgroups were identified,
204 which were composed of taxonomically (or functionally) consistent diet items that composed a
205 threshold representation within stomachs. Subgroups were used only if the category represented

206 a mean of at least 1% of total stomach contents for at least one species of fish. Dietary groupings
207 were used to compare inter-island differences of relative diet composition across trophic
208 groupings.

209 Based on the nature of differing diet items and digestion process, slightly different
210 definitions of relative composition were used across fish trophic groups. For the piscivore-
211 invertivores (*L. bohar, C. urodeta,* and *P. arcatus*), diet composition was described by estimating
212 the proportional weight of each diet category to the total weight of diet items removed from the
213 individual fish's stomach. The diet composition of planktivores (*P. bartlettorum* and *C.*
214 *margaritifer*) was described using a similar protocol, however, due to the small size of diet items
215 observed across diet categories, we used relative abundance of items rather than proportional
216 weight. Relative abundance was also used to characterize the diets of the three grazer-detritivores
217 (*S. aureus, A. nigricans,* and *C. marginatus*). Due to difficulties associated with classifying
218 partially digested algae to high taxonomic resolution, we assigned diet items to one of three algal
219 functional group categories, namely early stage algae (e.g., low-lying turf algae), late stage algae
220 (e.g., upright fleshy seaweeds), and calcified algae (e.g., algae that contained $CaCO_3$);
221 invertebrate, sand (detritus), and 'other' categories also were included in the diet assessment.
222 Stomach content analysis provides a valuable tool for describing the types of prey and general
223 feeding habits of consumers. However, this approach provides only a snapshot of feeding habits
224 and may not reflect the long-term diet of target species, especially for piscivore-invertivores that
225 can switch prey sources frequently or that consume items that are digested at different rates
226 (Hyslop 1980).

227 Complementing stomach contents analysis, we used stable isotope analysis ($\delta^{13}C$ and
228 $\delta^{15}N$) to obtain an integrated view of diets and evaluate relative position across species-island

229 combinations. This was accomplished by selecting 10 individuals from each species-island
230 combination included in the stomach contents assessments whenever possible (Table 1). A
231 section of muscle tissue (0.05-1.0 g) was removed from the left dorsal region of each fish and
232 samples were stored frozen (-20° C) and processed following standardized stable isotope
233 protocols (Michener and Lajtha 2007; Post 2002). Presenting mean values of $\delta^{13}C$ - $\delta^{15}N$ of an
234 organism or population in either single-plot or bi-plot space can provide important information
235 regarding relative trophic position, food web structure, and niche width (Layman et al. 2007;
236 Post 2002). To describe context-specific shifts in relative isotope position among species, we
237 focused our interpretation on the $\delta^{15}N$ values using single-plots across islands but we also
238 provide summaries of $\delta^{13}C$ values as bi-plots to complement $\delta^{15}N$ data and reinforce models of
239 relative trophic position observed across islands. Additional methodological details and data
240 interpretation are provided in Electronic Supplemental Material (Online Resource 1).

241 *Statistical Analyses*

242 To formally test the null hypothesis that the diets of individual fish species did not differ among
243 islands, we used a resampling approach that accounts for the multinomial (non-independent)
244 nature of percentage stomach content data. For example, the diet composition of individual fish
245 is the result of numerous multinomial choices made during foraging activities. Each item
246 consumed can be assigned to a diet category based on taxonomy (or functional group) and the
247 number of diet categories is determined by the operational level of dietary resolution. The total
248 percentage of each diet category represents an estimation of the multinomial probabilities for
249 foraging events made by an individual fish. Further, the total percentage of each diet category is
250 bound between 0% - 100% and is dependent on the percentage values of the other diet categories

observed during the assessment. As such, stomach contents data violate a number of assumptions of normality and independence required for many traditional statistical approaches.

To address the multinomial nature of diet data we used a tailored resampling routine following an analytical approach introduced previously (Barott et al. 2012). Consider a visualization in which data are plotted in n dimensions, where n is the number of diet categories. Mean relative diet composition for individuals from one island is calculated as the island-specific centroid of the data in n-dimensional space, and the mean for all individuals from across islands is calculated as the global centroid from all samples. The mean intercentroid distance among island samples was calculated by measuring the Euclidean distances between the centroids for each island from the global centroid. A resampling routine (10,000 iterations) was used to generate a null distribution of mean intercentroid distances, by repeatedly scrambling island affiliations of diet composition data from all individuals and calculating the intercentroid distance. The actual mean intercentroid distance was compared to this null distribution to test whether mean diets differed among islands for each species. If the null hypothesis of no difference among islands was rejected for data from a species, the procedure above was repeated individually for all pairs of islands to generate pairwise comparisons among each species-island combination; the null hypothesis for the post-hoc test was rejected if $p \leq 0.01$. This analytical procedure using Euclidean distances is robust, in most cases, across levels of aggregation of diet categories given that the approach does not *de facto* create higher sensitivity to increased number of functional groups. However, to assure empirically that the level of aggregation of diet categories did not affect conclusions, analyses and figures presented in the main text using high-resolution diet category subgroups are complemented by comparable analyses and figures with diet category subgroups lumped into course groupings (the latter presented in the Online

Resources). Notably, the results did not differ qualitatively between the two hierarchical categorizations of diets.

To test whether the relative $\delta^{15}N$ signal of individual fish species differed across islands, we used a single factor analysis of variance (ANOVA) treating island (5 levels) as the fixed factor. This was completed for all species-island combinations but recognizing *a prior*, that the planktivore, *P. bartlettorum* lacked one species-island combination due to biogeographic absence at Kingman. Tukey pairwise comparisons (planned contrasts between islands) were used to identify which species-island combinations differed in relative $\delta^{15}N$ space and examine consistencies among species and functional trophic groups. Our prediction was that foraging patterns within a species would remain consistent across environmental contexts and be reflected in the stable isotope signatures among species. All statistical analyses were completed using R version 3.0.1 and RStudio version 1.1.453 (R Development Core Team; www.r-project.org).

Results – The eight fish species included in this assessment spanned a range of body sizes and three functional trophic groups (Table 1). The two planktivores were the smallest species processed, and the piscivore-invertivore, *Lutjanus bohar*, was the largest species, with the total collection of fishes spanning a range of standard lengths (SL) from 1.55 cm to 61.50 cm. The remaining species ranged in size from 1.79 cm SL to 20.30 cm SL. Representative samples for stomach content analysis were obtained for all eight species-island combinations with the exception of *P. bartlettorum* which was not present at Kingman (Table 1). In some instances, the stomachs of a subset of species-island combinations were observed to be empty and the lack of stomach contents data was reflected in the reduced number of individuals reported as processed

296 (i.e., *L. bohar, C. urodeta,* and *A. nigricans*; Table 1). Stomachs contained food items in the
297 remaining species-island combinations and were processed accordingly.
298 Stomach contents from 730 specimens from eight coral reef fish species across the NLI
299 were examined to evaluate diet composition (Table 1). Coarse evaluation of stomach contents
300 revealed variability among species but food items observed in the stomachs were generally
301 distinct within functional trophic groups (Fig. 2; Online Resources). For example, the diets of
302 piscivore-invertivores consisted primarily of fishes (diet composition range: 28%-77%) and
303 decapod-crustaceans (diet composition range: 0%-46%) while the diets of planktivores consisted
304 primarily of copepods (diet composition range: 51%-81%) and to a lesser extent egg sacks (diet
305 composition range: 5%-26%) and foraminifera (diet composition range: 0%-17%; Fig. 2; Online
306 Resources). The diets of grazer-detritivores were the most variable within functional trophic
307 groupings with stomach contents primarily comprised of varying proportions of early stage
308 algae, (complex cylinders diet composition range: 6%-55% and filamentous algae diet
309 composition range: 11%-36%), sandy detritus (diet composition range: 3%-57%), and to a lesser
310 extent invertebrates (diet composition range: 0%-21%) and late stage algae (foliose algae diet
311 composition range: 0%-18% and calcified algae diet composition range: 0%-14%)(Fig. 2, Online
312 Resources). Some material in the guts was unidentifiable due to digestion process, resulting a
313 proportion of the mass being labeled as 'Other'. This unidentified group within the stomach
314 contents was most prominent in *L. bohar*, perhaps due to the longer gut passage time for larger
315 gut volumes. Removal of this group within the stomach contents results did not alter the
316 qualitative conclusions of stomach contents data presented.
317 Pairwise comparisons revealed that the diets of each piscivore-invertivore species was
318 indistinguishable among islands (Table 2). The mean weight of prey was positively related to the

319 mean size of the piscivore-invertivore species, and mean prey weight scaled approximately an
320 order of magnitude between each of the three piscivore-invertivore species (Online Resource 5).
321 These findings suggest that the prey field and foraging patterns among the piscivore-invertivores
322 remained consistent across islands regardless of the individual's body size. For the planktivores,
323 there was a lack of consistency in the diets among species across islands, but we found the
324 species-specific diet of *P. bartlettorum* to be consistent across 3 of the 4 islands where samples
325 were collected (Fig. 2; Table 2; Online Resources). In contrast, pairwise comparisons revealed a
326 substantial variation and a lack of consistency in the diets within the grazer-detritivore group
327 across islands (Table 2). However, there were some instances at the island level where the diets
328 of grazer-detritivores were similar (e.g., Kingman and Tabuaeran; Table 2). The variability and
329 lack of consistency in stomach contents across islands suggests that grazer-detritivores forage
330 generally across a diverse and trophically complex prey field particular to each island-species
331 combination.
332 A total of 383 samples were processed for bulk stable isotope analysis across each
333 species-island combination with a couple of exceptions. Several of the processed isotope samples
334 from Jarvis for the piscivore-invertivore, *L. bohar*, were outside of acceptable range and deemed
335 unusable, and the planktivore, *P. bartlettorum,* did not occur at Kingman. Graphical analysis of
336 stable isotopes ($\delta^{15}N$) revealed consistency in the relative positions of some species pairs in
337 isotopic space across islands (Fig. 3; Online Resources). The relative isotopic signatures of the
338 three piscivore-invertivore species appeared to be similar across islands decreasing in isotopic
339 space moving from north to south (Kingman to Jarvis) along the gradient of oceanic primary
340 production. Notably, beyond relative isotopic signature, the actual mean isotopic signature
341 among the three species of piscivore-invertivore never differed by more than 1.5‰. The

342 planktivores also appeared to follow the same decreasing trend but exhibited more variability
343 among species-island combinations. In contrast the grazer-detritivores revealed no clear pattern
344 or consistency in stable isotopes ($\delta^{15}N$) among species across islands with the greatest variability
345 observed at the islands furthest from the equator.

346 Examining the isotopic patterns for species-island combinations in more detail revealed
347 significant differences (<0.001) in the $\delta^{15}N$ values for all species across the NLI (Table 3).
348 Pairwise comparisons provided insights into species-specific patterns within each functional
349 trophic group (Table 4). For the piscivore-invertivores, pairwise comparisons of $\delta^{15}N$ signatures
350 revealed similarity in the integrated diets between *C. urodeta* and *P. arcatus* across all five
351 islands ($p \leq 0.01$; Table 4). *L. bohar* $\delta^{15}N$ signatures were also similar to the other piscivore-
352 invertivores at Kingman and Palmyra but not for the islands further south. The integrated $\delta^{15}N$
353 signatures of the planktivores were consistent across all islands where both species were present.
354 In contrast, there were limited-to-no consistent patterns in $\delta^{15}N$ values for the grazer-detritivores
355 across the NLI. Jarvis was the only island where $\delta^{15}N$ signatures were similar across all three
356 species. For the remaining species-island combinations, the results were variable across species
357 suggesting inconsistencies in the integrated diets among grazer-detritivores (Table 4).
358
359 **Discussion –** Coral reef fishes are exceptionally diverse and represent a model system to explore
360 relative foraging habits of species across gradients of environmental context. Using stomach
361 contents and stable isotope analyses, we found evidence of foraging consistency among common
362 coral reef fishes from the central Pacific. However, these patterns were distinct between putative
363 functional trophic groupings. An examination of stomach contents revealed the diets of focal
364 species to be distinct among functional trophic groups, as expected based on assignments from

365 web-based (i.e., fishbase.org) and published references (Myers 1999; Randall 2005). For
366 instance, fishes within the piscivore-invertivore group preyed upon fishes and mobile
367 invertebrates, the planktivores preyed upon microscopic plankton from the water column, and the
368 grazer-detritivores primarily foraged upon algae, sandy detritus, and micro-invertebrates. Our
369 findings are consistent with an established natural historical perspective suggesting that variation
370 in the foraging ecologies observed among coral reef fishes is driven by the distinction of
371 functional roles and the manner in which groups of fishes exploit distinct energetic resources.
372 By design, we focused analyses on patterns of inter-island variation in foraging,
373 contrasting variability of multiple species of fish within these three functional trophic groups.
374 Using data on both short-term (stomach contents) and longer-term (somatic stable isotopic
375 composition) foraging patterns, we find that species have differential patterns of variation across
376 the northern Line Islands. The species of grazer-detritivore (*Stegastes aureus, Acanthurus*
377 *nigricans*, and *Ctenochaetus marginatus*) exhibited the greatest variation in stomach contents
378 and stable isotope ($\delta^{15}N$) values across islands. Post-hoc estimates of stomach contents reveal
379 variable groupings of diet similarity across the three species of grazer-detritivore (Table 2),
380 suggesting that the determinants of diets at an island differ among the species (e.g., due to
381 differences in species-specific foraging preferences and island-specific availability of food
382 items). The more integrated measure of foraging, somatic tissue $\delta^{15}N$, shows more qualitative
383 consistency in values across islands (each species showing highest $\delta^{15}N$ values at Teraina, the
384 island at the middle latitude in this study; Fig. 3b, Table 4), but a consistent cause for this
385 similarity across species is not obvious. Notably, the benthic habitats are quite variable in algal
386 and other composition across this region, due to both oceanographic forcing and alterations of

387 the fish assemblage structure due to fishing (DeMartini et al. 2008; Sandin et al. 2008; Smith et
388 al. 2016).

389 There was notably less estimated variation in foraging across islands for the species of
390 planktivore, and the least for the species of piscivore-invertivore. Review of the stomach
391 contents analyses showed some inter-island differences in prey composition for the two species
392 of planktivore (Table 2); *Chromis margaritifer* showed different relative abundances of prey for
393 each island (except for Kingman, which was indistinguishable from all islands aside from
394 Jarvis), while *Pseudanthias bartlettorum* showed similar relative abundances for all islands,
395 except for Jarvis. The stomach contents of each species piscivore-invertivore (*Lutjanus bohar*,
396 *Cephalopholis urodeta*, and *Paracirrhites arcatus*) were indistinguishable across islands (Table
397 2). Notably, stomach contents data have limited taxonomic resolution of prey, highlighted clearly
398 by the 'fish' prey category within piscivore-invertivore that may contain any of hundreds of
399 potential prey fish species. It is possible that results at the functional-group resolution presented
400 here belie taxonomic differences of prey among islands. Finer analyses of stomach contents at
401 taxonomic- or species-level would require advances in stomach contents methodology (e.g.,
402 metabarcoding) and dramatic increases in numbers of individuals sampled.

403 For each species of planktivore and piscivore-invertivore, stable isotope analysis showed
404 a consistent pattern across islands, with more equatorial islands systematically associated with
405 similar or lower somatic tissue $\delta^{15}N$ estimates relative to more northern islands (Table 4, Fig. 3).
406 When examining the results of stable isotope estimates for species of piscivore-invertivore across
407 islands, we observed evidence of latitudinal consistency that appeared to be linked to the north-
408 south gradient of oceanic primary production (Fig. 1; Online Resources). In the NLI, regional
409 and nearshore biogeophysical processes deliver essential energetic subsidies to shallow coral reef

410 communities (Gove et al. 2016). The frequency and magnitude of these events increase with
411 proximity to the equator and directly influences the marine biogeochemical cycle (Altabet 2001;
412 Gove et al. 2016). Specifically, internal waves and localized upwelling deliver sub-thermocline
413 15N-depleted inorganic nitrogen that directly affects the basal source signature of $\delta^{15}N$ whereby,
414 isotope values are generally lower near the equator due to increased availability and, preferential
415 biological uptake and fractionation of lighter NO^-_3 (see Fig. 4, bottom panel in Altabet 2001). In
416 our study, the $\delta^{15}N$ values of the piscivore-invertivores decreased with proximity to the equator
417 and suggests that the diets are linked allochthonous sources of oceanic primary production (Fig.
418 4).

419 Another surprising finding was that the $\delta^{15}N$ values of the three species of piscivore-
420 invertivores were similar across all 5 islands despite exhibiting distinct size-structured diets and
421 differing in body size by an order of magnitude (Fig. 3; Online Resource 8). The observed size
422 structuring in the diets of the piscivore-invertivores was not surprising considering the ubiquity
423 of gape limitation associated with morphological constraints in aquatic food webs (Hairston and
424 Hairston 1993; Romanuk et al. 2011). However, the consistency in the $\delta^{15}N$ values across species
425 was contrary to the common expectation of a positive scaling relationship between relative
426 trophic position and body size in coral reef food webs (Jennings et al. 2001; Romanuk et al.
427 2011). While we recognize that the results of pairwise comparisons indicated a lack of
428 quantitative consistency in the $\delta^{15}N$ values of the piscivore-invertivores across islands (Table 4),
429 when examining the mean $\delta^{15}N$ values of the three piscivore-invertivores within each island we
430 observed the values to be within 1.5‰ $\delta^{15}N$ of each other and are unlikely to be ecologically
431 relevant (Fig. 3). Recall that most assessments of relative trophic position suggest that one
432 trophic level is matched with a 2.5-4.0‰ enrichment in $\delta^{15}N$ (Post 2002).

433 The latitudinal consistency of the stable isotope estimates combined with the size
434 structuring in the diets suggests that on central Pacific coral reefs, the diets of piscivore-
435 invertivores, regardless of body size and feeding ecology, reveal close trophic similarities and
436 appear linked closely to basal planktonic energetic resources. Further, these data provide
437 empirical dietary evidence of tight trophic linkages from lower to higher functional trophic levels
438 (planktivore to piscivore-invertivore, without intermediate trophic steps) consistent with
439 hypotheses generated from fish biomass distributional patterns explored across the Indian Ocean
440 (Graham et al. 2017). Our findings suggest that both larger and smaller bodied piscivore-
441 invertivores derive much of their energy by preying on species closely linked to basal resources
442 (e.g., planktivores feeding near to source of oceanic primary production). Such tight linkages
443 with basal sources of oceanic primary production can reduce the number of steps between
444 trophic levels and may be a mechanism contributing to increased energetic efficiency within the
445 trophic ecology of some reef fish assemblages.
446 In contrast to the piscivore-invertivores, the $\delta^{15}N$ values of the grazer-detritivores did not
447 track estimates of oceanic primary production along the north-south latitudinal gradient (Fig. 3).
448 Instead, we found the feeding ecologies of the grazer-detritivores to be distinct among species
449 and this distinction was reflected in their diets and stable isotopic values (Fig. 2; Fig. 3; Online
450 Resources). For example, the stable isotope values of *S. aureus* and *C. marginatus* exhibit greater
451 enrichment in ^{15}N, likely a result of consuming a greater proportion of diet items (i.e.,
452 invertebrates and detritus) that are themselves enriched in $\delta^{15}N$ compared to common groups of
453 algae consumed by grazer-detritivores. In the case of *C. marginatus*, $\delta^{15}N$ values were equal to
454 or often greater than the $\delta^{15}N$ values of the piscivore-invertivores, which is consistent with a
455 feeding mode that includes coprophagy and the consumption of detritus (McMahon et al. 2016).

456 Further, the presence of physiological food processing mechanisms, including gut fermentation
457 and microbial activity can contribute to higher rates of trophic fractionation and result in higher
458 $\delta^{15}N$ values than expected in some grazer-detritivores (Mill et al. 2007). The variability in the
459 diets and isotopic values observed among grazer-detritivores highlights the complex nature of
460 this benthic-foraging group (Choat et al. 2004; Clements et al. 2009) as well as the prevalence of
461 omnivory and coprophagy in coral reef ecosystems (Crossman et al. 2005; McMahon et al.
462 2016).

463 Across islands, we found a significant effect of oceanic primary production (estimated as
464 concentration of water-column chlorophyll-*a*) on the $\delta^{15}N$ stable isotopic values of tissue from
465 piscivore-invertivores with $\delta^{15}N$ values decreasing with increasing oceanic primary production
466 (Online Resource 8). Interestingly, the isotope values of the piscivore-invertivores and
467 planktivores were consistent across islands with the piscivore-invertivores tracking between 2.5
468 and 4.0‰ greater in $\delta^{15}N$ than the isotopic values of the mean of the two species of planktivore
469 surveyed as would be expected for stepwise enrichment between trophic groups (Post 2002) (Fig.
470 3; Online Resource 9). While it was somewhat obvious that the diet and isotopic signature of
471 planktivores was linked to oceanic energetic subsidies (i.e., copepods comprised >65% of their
472 diet based on stomach contents), the consistency in diet and isotope position observed for the
473 piscivore-invertivores was rather surprising. Our results suggest that piscivore-invertivores
474 across body sizes primarily exploit prey species positioned low in the food web and derived from
475 allochthonous sources of oceanic primary production.

476 It should not be surprising that coral reef communities should support a wide range of
477 species with diverse trophic ecologies that often exploit varying energetic resources. Our
478 observations indicate that coral reefs exhibit relatively consistent patterns in food web structure,

but they are not necessarily the same as those expected on the basis of simple concepts of niche differentiation (e.g., larger taxa systematically eating at higher trophic level). Our results suggest that planktivores and piscivore-invertivores both seemingly exploit prey derived primarily from sources of oceanic primary production. In contrast, grazer-detritivores on coral reefs support diets that are more complicated, with species exploiting a diverse prey field linked not only to benthic primary production but also linked indirectly to sources of oceanic primary production as a result of autochthonous recycling. The topological pathways by which energetic resources are transferred through complex communities has important implications for the function and stability of coral reef food webs, and we may need to change the way that we think about these systems if we aim to incorporate multi-species approaches into coral reef fisheries management. In the northern Line Islands, exploiting energetic resources derived from sources of oceanic primary production likely increases trophic productivity among piscivore-invertivores (Rooney and McCann 2012) and may serve as one of the mechanisms for why intact coral reef ecosystems can support such a high biomass of piscivore-invertivores towards the top of the food web (McCauley et al. 2018; Sandin and Zgliczynski 2015). Together these findings provide important insight into the foraging patterns of coral reef fish assemblages and should inspire myriad research questions and field experiments that aim to increase our understanding of the influence environmental gradients in driving the trophic dynamics of hyperdiverse aquatic ecosystems.

Acknowledgments – This work was conducted with the support of the Moore Family Foundation and several donors to the Scripps Institution of Oceanography. We thank the Republic of Kiribati, Environment and Conservation Division and the U.S. Fish and Wildlife Service (USFWS) for permission to complete this work. For logistical support we thank the

officers and crew of the M/V *Hanse Explorer* and the staff of the Nature Conservancy at Palmyra Atoll. We thank Zach Caldwell, Joe Laughlin, Kyle Koyanagi, and Stephan Charrette for invaluable assistance in the field and Bruce Deck and Brice Semmens for assistance with stable isotope sample preparation, analysis, and insightful discussions.

References

Adam TC, Kelley M, Ruttenberg BI, Burkepile DEJO (2015) Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. 179:1173-1185

Altabet MA (2001) Nitrogen isotopic evidence for micronutrient control of fractional NO utilization in the equatorial Pacific. Limnol Oceanogr 46:368-380

Barott KL et al. (2012) Natural history of coral− algae competition across a gradient of human activity in the Line Islands. Marine Ecology Progress Series 460:1-12

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007-1012

Bellwood D, Wainwright P, Fulton C, Hoey A (2006) Functional versatility supports coral reef biodiversity. Proceedings of the Royal Society B: Biological Sciences 273:101

Choat J, Robbins W, Clements K (2004) The trophic status of herbivorous fishes on coral reefs. Mar Biol 145:445-454

Clements KD, Raubenheimer D, Choat JH (2009) Nutritional ecology of marine herbivorous fishes: ten years on. Functional Ecology 23:79-92

Crossman DJ, Choat JH, Clements KD (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. Marine Ecology Progress Series 296:129-142

Deb D (1997) Trophic uncertainty vs parsimony in food web research. Oikos:191-194

DeMartini EE (1996) Sheltering and foraging substrate uses of the arc-eye hawkfish Paracirrhites arcatus (Pisces: Cirrhitidae). B Mar Sci 58:826-837

DeMartini EE, Friedlander AM, Sandin SA, Sala E (2008) Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. Mar Ecol-Prog Ser 365:199-215. doi: 10.3354/Meps07501

Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151-1157

Gove JM et al. (2016) Near-island biological hotspots in barren ocean basins. Nature Communications 7. doi: 10.1038/ncomms10581

Graham NA et al. (2017) Human disruption of coral reef trophic structure. Curr Biol 27:231-236

Hairston NG, Hairston NG (1993) Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. The American Naturalist 142:379-411

Hempson TN, Graham NAJ, MacNeil MA, Williamson DH, Jones GP, Almany GR (2017) Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecology and Evolution 7:2626-2635. doi: 10.1002/ece3.2805

Hyslop EJ (1980) Stomach Contents Analysis - a Review of Methods and Their Application. J Fish Biol 17:411-429

Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross species relationships between body size and trophic level belie powerful size based trophic structuring in fish communities. Journal of Animal Ecology 70:934-944

Kramer M, Bellwood O, Bellwood D (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral Reefs 32:575-583

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE, Suding K (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters 10:937-944

552 Lukoschek V, McCormick MIJMB (2001) Ontogeny of diet changes in a tropical benthic
553 carnivorous fish, Parupeneus barberinus (Mullidae): relationship between foraging
554 behaviour, habitat use, jaw size, and prey selection. 138:1099-1113
555 Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and
556 trophic coupling in two marine apex predators. Journal of Animal Ecology 80:294-305
557 McCauley DJ et al. (2018) On the prevalence and dynamics of inverted trophic pyramids and
558 otherwise top-heavy communities. Ecol Lett. doi: 10.1111/ele.12900
559 McCauley DJ, Young HS, Dunbar RB, Estes JA, Semmens BX, Micheli F (2012) Assessing the
560 effects of large mobile predators on ecosystem connectivity. Ecol Appl 22:1711-1717
561 McMahon KW, Thorrold SR, Houghton LA, Berumen ML (2016) Tracing carbon flow through
562 coral reef food webs using a compound-specific stable isotope approach. Oecologia
563 180:809-821
564 Michener RH, Lajtha K (2007) Stable isotopes in ecology and environmental science. Blackwell,
565 Oxford
566 Mill A, Pinnegar J, Polunin N (2007) Explaining isotope trophic‐step fractionation: why
567 herbivorous fish are different. Functional Ecology 21:1137-1145
568 Motta PJ (1988) Functional morphology of the feeding apparatus of ten species of Pacific
569 butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. Environ
570 Biol Fish 22:39-67. doi: 10.1007/bf00000543
571 Myers RF (1999) Micronesian reef fishes: a field guide for divers and aquarists. Coral Graphics,
572 Barrigada, Guam
573 Plaisance L, Knowlton N, Paulay G, Meyer CJCR (2009) Reef-associated crustacean fauna:
574 biodiversity estimates using semi-quantitative sampling and DNA barcoding. 28:977-986

575 Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and
576 assumptions. Ecology 83:703-718
577 Randall JE (2005) Reef and shore fishes of the South Pacific; New Caledonia to Tahiti and the
578 Pitcairn Islands. Univeristy of Hawaii Press, Honolulu, Hawaii
579 Romanuk TN, Hayward A, Hutchings JA (2011) Trophic level scales positively with body size
580 in fishes. Global Ecology and Biogeography 20:231-240. doi: 10.1111/j.1466-
581 8238.2010.00579.x
582 Rooney N, McCann KS (2012) Integrating food web diversity, structure and stability. Trends
583 Ecol Evol 27:40-46
584 Ruttenberg BI et al. (2011) Predator-Induced Demographic Shifts in Coral Reef Fish
585 Assemblages. Plos One 6. doi: e21062
586 Sandin S, Zgliczynski B (2015) Inverted trophic pyramids. In: Mora C (ed) Ecology of Fishes on
587 Coral Reefs. Cambridge University Press, U.K., pp 247-251
588 Sandin SA et al. (2008) Baselines and degradation of coral reefs in the northern Line Islands.
589 Plos One 3:e1548. doi: 10.1371/journal.pone.0001548
590 Silveira CB et al. (2017) Microbial processes driving coral reef organic carbon flow. 41:575-595
591 Smith JE et al. (2016) Re-evaluating the health of coral reef communities: baselines and
592 evidence for human impacts across the central Pacific Proc. R. Soc. B, vol. 283. The
593 Royal Society, p 20151985
594 Somera TM et al. (2016) Energetic differences between bacterioplankton trophic groups and
595 coral reef resistance. J Proc. R. Soc. B 283:20160467

St John J (1999) Ontogenetic changes in the diet of the coral reef grouper Plectropomus leopardus (Serranidae): patterns in taxa, size and habitat of prey. Marine Ecology Progress Series 180:233-246

Stella JS, Jones GP, Pratchett MSJCR (2010) Variation in the structure of epifaunal invertebrate assemblages among coral hosts. 29:957-973. doi: 10.1007/s00338-010-0648-8

Wainwright P, Bellwood D (2002) Ecomorphology of feeding in Coral reef fishes. In: Sale P (ed) Coral reef fishes: dynamics diversity in a complex ecosystem. Academic Press, p 33

Williams GJ et al. (2018) Biophysical drivers of coral trophic depth zonation. 165:60

Wood CL, Sandin SA, Zgliczynski B, Guerra AS, Micheli F (2014) Fishing drives declines in fish parasite diversity and has variable effects on parasite abundance. Ecology 95:1929-1946

Wyatt A, Waite A, Humphries S (2012) Stable isotope analysis reveals community-level variation in fish trophodynamics across a fringing coral reef. Coral Reefs 31:1029-1044

Zgliczynski BJ, Sandin SA (2017) Size-structural shifts reveal intensity of exploitation in coral reef fisheries. Ecological Indicators 73:411-421

611 **Table 1.** Characteristics of the eight coral reef species identifying sample sizes for stomach
612 content and stable isotope (in parentheses) analyses by island: KIN = Kingman; PAL = Palmyra;
613 TER = Teraina; TAB = Tabuaeran; and JAR = Jarvis. The regional contribution of each species
614 to total mean fish abundance and biomass is given as a percentage (%). Satellite derived
615 estimates of oceanic primary production (Chlorophyll-*a*) are provided for each island. Values for
616 Chlorophyll-*a*, abundance, and biomass are means with standard error given in parentheses.
617 Sizes of fishes are given in standard length and NP denotes that the species was not present at the
618 island. Samples supplementing the 2010 field expedition are identified with an Asterix (* =
619 2006; and ** = 2011).
620

621

Functional Group, Species	Size Range Collected (cm)	Mean Size Collected (cm)	Mean Size Processed (cm)	KIN	PAL	TER	TAB	JAR	Contribution to: Fish Abundance (%)	Contribution to: Fish Biomass (%)
Piscivore-invertivores										
Lutjanus bohar	10.15-61.50	40.33	44.27	20 (10)	20 (10)	9 (10)	7 (10)	4 (3)	0.31	16.71
Cephalopholis urodeta	7.30-18.82	13.63	14.92	15 (10)	20 (10)	20 (10)	20 (10)	20 (10)	0.38	0.91
Paracirrhites arcatus	3.33-10.60	7.58	8.64	20 (10)	20 (10)*	20 (10)	20 (10)	20 (10)	0.61	0.29
Planktivores										
Pseudanthias bartlettorum	1.99-5.92	3.66	4.54	NP	20 (10)**	20 (10)	20 (10)	20 (10)	7.92	0.35
Chromis margaritifer	1.55-6.57	4.14	4.84	20 (10)	20 (10)*	20 (10)	20 (10)	20 (10)	19.57	0.77
Grazers-detritivores										
Stegastes aureus	1.79-8.70	6.14	7.36	20 (10)	20 (10)	20 (10)	20 (10)	20 (10)	0.56	0.29
Acanthurus nigricans	5.80-18.50	12.38	15.45	20 (10)	15 (10)*	20 (10)	20 (10)	20 (10)	0.73	2.63
Ctenochaetus marginatus	2.45-20.30	12.19	14.31	20 (10)	20 (10)	20 (10)	20 (10)	20 (10)	0.43	1.45
			TOTAL	135 (70)	155 (80)	149 (80)	147 (80)	144 (73)	30.50	23.41
			Mean Chlorophyll-*a* (mg m^{-3})	0.21	0.18	0.17	0.16	0.12		
				(0.001)	(0.001)	(0.002)	(0.002)	(0.002)		
			Total Reef Fish Abundance (# m^{-2})	27.79	11.82	6.61	7.56	3.52		
				(3.74)	(0.70)	(0.61)	(0.80)	(0.18)		
			Total Mean Reef Fish Biomass (g m^{-2})	412.02	112.29	159.51	90.45	225.86		
				(98.08)	(6.26)	(18.28)	(13.98)	(27.22)		
			Total Mean Top-predator Biomass (g m^{-2})	256.62	29.53	37.31	12.26	155.55		

622

623 **Table 2.** Output results of pairwise comparisons using a multinomial approach to examine
624 stomach contents of eight species across the Northern Line Islands. Significant difference based
625 on $p \leq 0.01$. NP denotes that the species was not present at the island. Dashes indicate stomachs
626 of sampled individuals were observed to be empty.
627

Functional Group **Species**	**Kingman**	**Palmyra**	**Teraina**	**Tabuaeran**	**Jarvis**
Piscivore-invertivores					
Lutjanus bohar	A	A	A	A	--
Cephalopholis urodeta	A	A	A	A	A
Paracirrhites arcatus	A	A	A	A	A
Planktivores					
Pseudanthias bartlettorum	NP	A	A	A	B
Chromis margaritifer	A, B, C	A	B	C	D
Grazer-detritivores					
Stegastes aureus	A	A, C	A	B	C
Acanthurus nigricans	A	B	B, C	B	C
Ctenochaetus marginatus	A,B,C	A, C	A	B	C

628

Table 3. Output results of one-way analysis of variance (ANOVAs) testing the effect of Island on the $\delta^{15}N$ values of key coral reef fish across multiple functional trophic groups.

Functional Group **Species**	**MS**	**df**	***F*-value**	***p*-value**
Piscivore-invertivores				
Lutjanus bohar	5.50	4	14.35	<0.001
Cephalopholis urodeta	15.48	4	137.90	<0.001
Paracirrhites arcatus	14.24	4	121.00	<0.001
Planktivores				
Pseudanthias bartlettorum	8.20	3	19.44	<0.001
Chromis margaritifer	28.31	4	46.77	<0.001
Grazer-detritivores				
Stegastes aureus	12.79	4	81.98	<0.001
Acanthurus nigricans	3.10	4	13.29	<0.001
Ctenochaetus marginatus	7.09	4	16.29	<0.001

Table 4. Output results of pairwise comparisons using Tukey honest significant difference (HSD) to examine consistency in $\delta^{15}N$ of eight species of coral reef fishes across islands. Significance based on $p \leq 0.01$. NP denotes that the species was not present at the island.

Functional Group **Species**	**Kingman**	**Palmyra**	**Teraina**	**Tabuaeran**	**Jarvis**
Piscivore-invertivores					
Lutjanus bohar	A	A	A, B	B	C
Cephalopholis urodeta	A	A	B	C	D
Paracirrhites arcatus	A	A	B	C	D
Planktivores					
Pseudanthias bartlettorum	NP	A	B	B	B
Chromis margaritifer	A	A	B	B	B
Grazer-detritivores					
Stegastes aureus	B, C	A	A	B	C
Acanthurus nigricans	B, C	B	A	B	B
Ctenochaetus marginatus	C	A	A	A	B

639 **Figures**

640 **Fig. 1.** Map of the northern Line Islands identifying the three remote islands (Kingman, Palmyra
641 and Jarvis) and two inhabited islands (Teraina and Tabuaeran) that served as study sites. Long-
642 term (10 years) estimate of mean chlorophyll-*a* used as a proxy of phytoplankton biomass for the
643 region highlighting the south to north gradient of oceanic primary production observed across
644 study sites. (color figure online)

645

646 **Fig. 2.** Percent composition of dietary category subgroupings observed in the stomachs of the:
647 (a) piscivore-invertivores (*Lutjanus bohar, Cephalopholis urodeta, Paracirrhites arcatus*); (b)
648 planktivores (*Pseudanthias bartlettorum* and *Chromis margaritifer*); and (c) grazers-detritivores
649 (*Stegastes aureus, Acanthurus nigricans, Ctenochaetus marginatus*) across islands. Island codes
650 are as follows: KIN = Kingman; PAL = Palmyra; TER = Teraina; TAB = Tabuaeran; JAR =
651 Jarvis. Blanks indicate missing diet data for species-island combination and "NP" indicates
652 species-island combination where a species was not present at the island. At Jarvis, the guts of *L.*
653 *bohar* were empty. Letters above plots indicate results of multinomial pairwise comparisons.
654 (N=20 for all species-island combinations with exception of the following: *L. bohar*, Teraina
655 N=9, Tabuaeran N=7, Jarvis N=4; *C. urodeta*, Kingman N=15; *A. nigricans*, Palmyra N=15)
656 (color figure online).

657

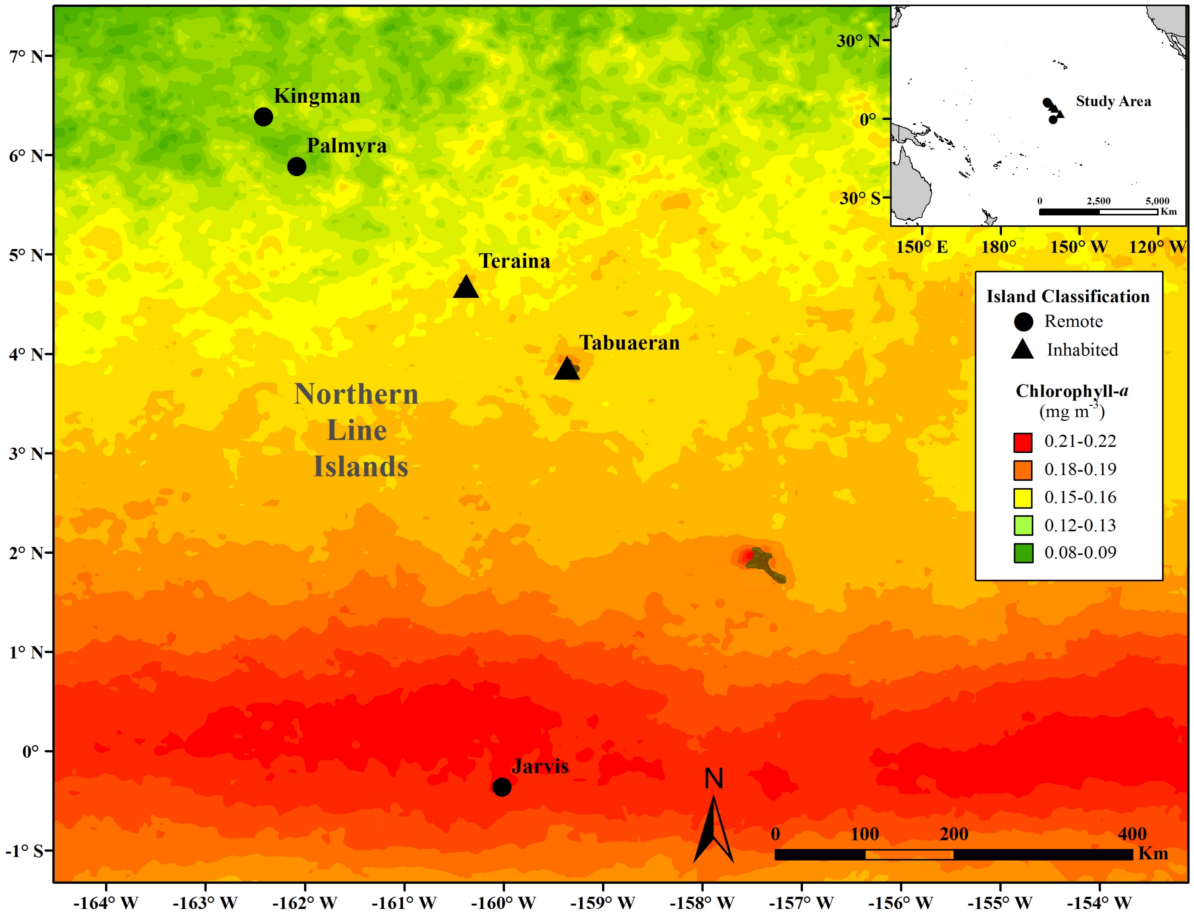
658 **Fig. 3.** Values of $\delta^{15}N$ for coral reef fish species plotted across the northern Line Islands in north
659 to south orientation (left to right). Plot (a) includes focal species representing piscivore-
660 invertivore and planktivore functional trophic groups while plot (b) includes focal species
661 representing the grazer-detritivore functional trophic group. All values are mean and ± 1 standard

662 deviation. (N=10 for all species-island combinations with exception of the following: *L. bohar*,

663 Jarvis N=3) (color figure online).

664

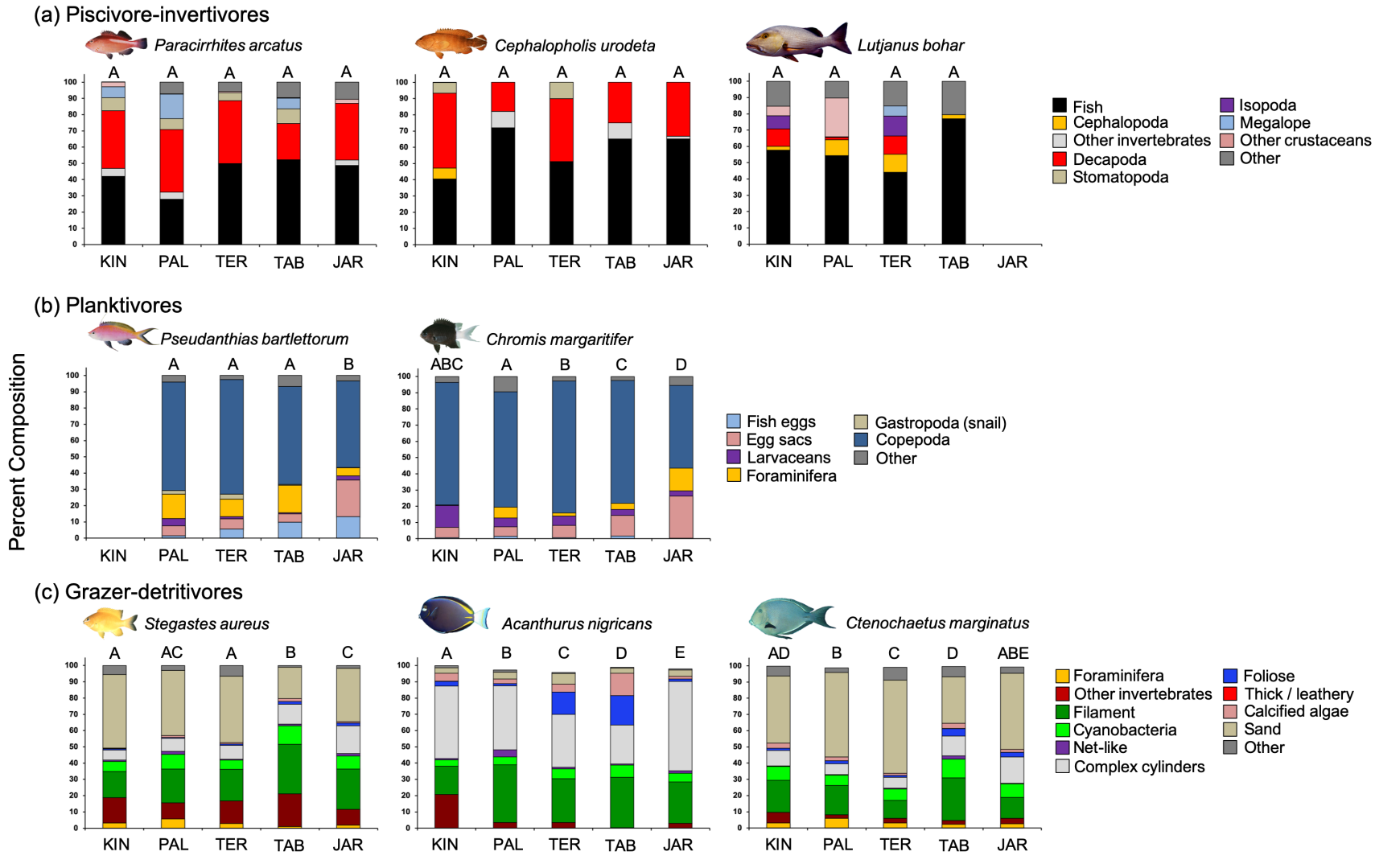
665 **Fig. 1.**



666

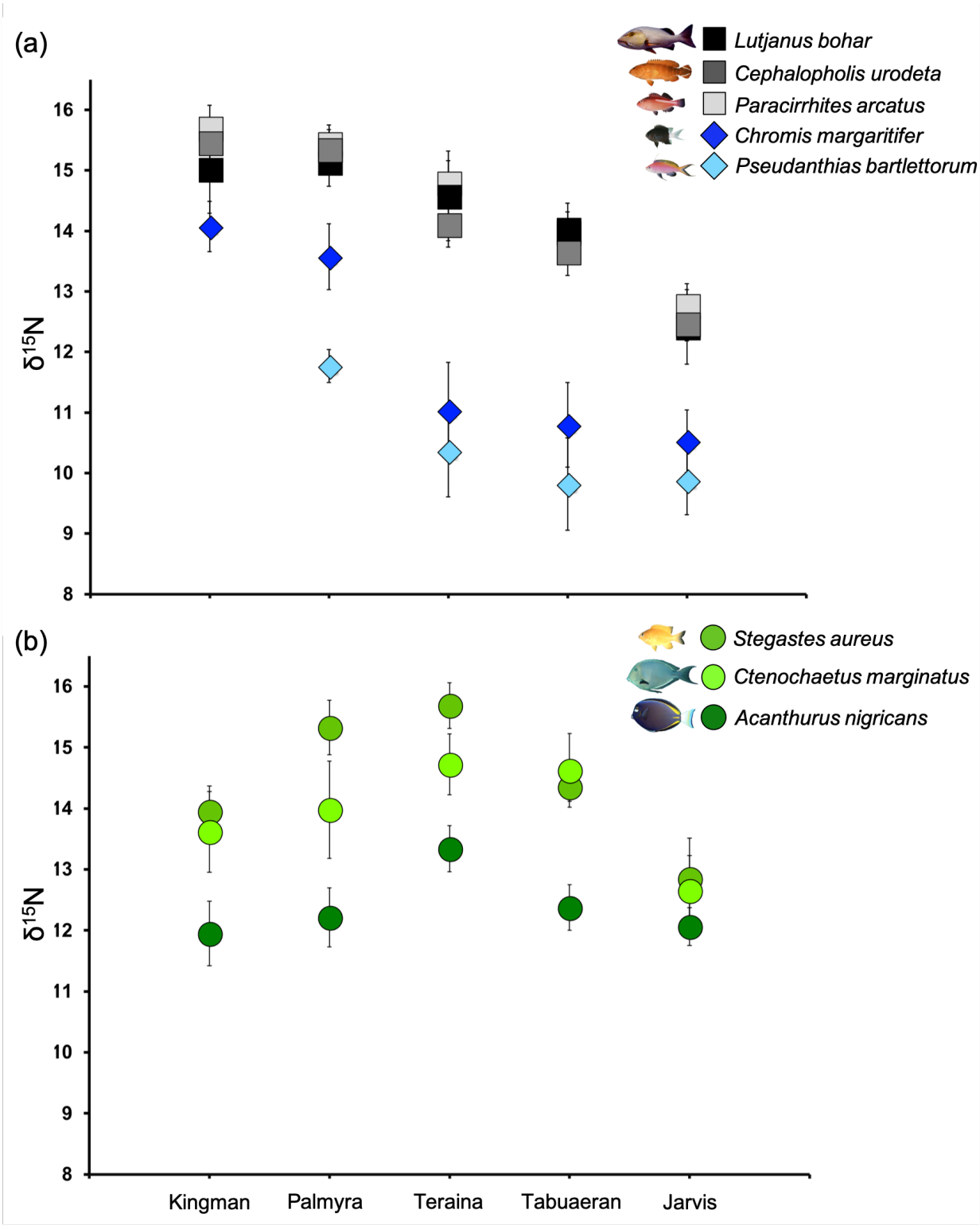
667

668 **Fig. 2.**


(a) Piscivore-invertivores
Paracirrhites arcatus
Cephalopholis urodeta
Lutjanus bohar
A A A A A
KIN PAL TER TAB JAR
Fish
Cephalopoda
Other invertebrates
Decapoda
Stomatopoda
Isopoda
Megalope
Other crustaceans
Other
(b) Planktivores
Pseudanthias bartlettorum
Chromis margaritifer
A A A B
ABC A B C D
Percent Composition
Fish eggs
Egg sacs
Larvaceans
Foraminifera
Gastropoda (snail)
Copepoda
Other
(c) Grazer-detritivores
Stegastes aureus
Acanthurus nigricans
Ctenochaetus marginatus
A AC A B C
A B C D E
AD B C D ABE
Foraminifera
Other invertebrates
Filament
Cyanobacteria
Net-like
Complex cylinders
Foliose
Thick / leathery
Calcified algae
Sand
Other

669

670 **Fig. 3**


(a)
Lutjanus bohar
Cephalopholis urodeta
Paracirrhites arcatus
Chromis margaritifer
Pseudanthias bartlettorum
δ15N
16
15
14
13
12
11
10
9
8
(b)
Stegastes aureus
Ctenochaetus marginatus
Acanthurus nigricans
δ15N
16
15
14
13
12
11
10
9
8
Kingman
Palmyra
Teraina
Tabuaeran
Jarvis

671

Electronic Supplemental Materials (ESM) – Online Resources

Foraging consistency of coral reef fishes across environmental gradients in the central Pacific

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Online Resource 1. Additional details regarding the study system and the methods used to examine dietary consistency across the Line Islands.

Study sites

Teraina and Tabuaeran are part of the Republic of Kiribati and contain human population densities ranging from several hundred to several thousand people (DeMartini et al. 2008, Sandin et al. 2008). Fishing serves as the primary source of income for island residents with hook and line, spearfishing, and hand-nets being the most common methods. In contrast, Kingman, Palmyra and Jarvis are uninhabited U.S. possessions protected from fishing as part of the U.S. Pacific Remote Islands Marine National Monument and previously protected as U.S. National Wildlife Refuges (Maragos et al. 2008, Bush 2009). As such these protected islands contain some of the most intact coral reef ecosystems in the Pacific (DeMartini et al. 2008, Sandin et al. 2008). Efforts to compare coral reef fish assemblages across the northern Line Islands have revealed stark differences between inhabited and uninhabited islands (DeMartini et al. 2008, Sandin et al. 2008). At uninhabited islands, total fish biomass is 2-4 times higher than at inhabited islands, with top-predators comprising the highest proportions of fish biomass. Conversely, fish assemblages at inhabited islands are comprised of smaller-bodied species from lower-trophic levels. Importantly, there is only limited evidence of prey release associated with changes in top-predator density (DeMartini et al. 2008, Sandin et al. 2010).

The northern Line Islands are also exposed to a latitudinal gradient of oceanographic primary production, whereby sea surface temperature increases and nutrient concentrations decrease with increasing latitude and distance from the equator (Altabet 2001, Sandin et al. 2008, Gove et al. 2013, Gove et al. 2016). At the regional scale, Jarvis and to a lesser extent Tabuaeran,

are influenced by upwelled nutrient-rich waters of the westward-flowing South Equatorial Current and the eastward-flowing Equatorial Undercurrent, while Kingman, Palmyra, and Teraina are geographically located in the path of the warmer oligotrophic flow of the North Equatorial Countercurrent. Additionally, islands within proximity of the equator are influenced by localized upwelling events as a result of the eastward flowing Equatorial Undercurrent coming into contact with steep island topography (Gove et al. 2006). We use satellite-derived (MODIS) estimates of chlorophyll-*a* (mg m^{-3}) as a proxy for nearshore oceanographic primary production using a masking routine to omit any compromised data associated with island or lagoon reflectance. Means were calculated by averaging eight-day chlorophyll-*a* values for each island over a ten-year time period (2005-2015). A masking routine was used to estimate the nearshore chlorophyll-*a* values along the 30 m isobath or a distance of 250m from the reef crest around each island and to omit any contaminated data associated with island or lagoon reflectance inshore of the 30-m isobath or directly adjacent to each pixel.

Stomach Content Analysis

Approaches used to identify trophic position or niche width in marine systems have traditionally relied on stomach content analysis (Hyslop 1980, Bearhop et al. 2004), which offers an invaluable tool for identifying the types of prey and the general feeding habits of a consumer (Randall 1967). We followed these traditional approaches to evaluate the relative contribution of prey items to the diet of each targeted species we used stomach content analyses. For the piscivore-invertivores (*L. bohar*, *C. urodeta*, and *P. arcatus*), we removed all stomach contents and weighed each food item individually to create a mean weight of item consumed (all food items combined). To characterize diet composition, we estimated what proportion of this total

weight was made up of different prey items. Prey items were defined as broad taxonomic groups. For the planktivores (*C. margaritifer* and *P. bartlettorum*), diet composition was based on the relative abundance of food items in the stomach, again assigned to broad taxonomic groups. For the grazer-detritivores (*S. aureus, A. nigricans*, and *C. marginatus*), diet composition was, like the planktivores, based on relative abundance of food items in the stomach. However, due to the difficulty of identifying algae that have undergone partial digestion to a high taxonomic resolution, all algae were assigned to one of three functional group categories, namely early stage algae (e.g., low-lying turf algae), late stage algae (e.g., upright fleshy seaweeds), and calcified algae (e.g., algae that contained $CaCO_3$). Additionally for herbivores, food items were also classified into the invertebrate and sand categories.

Stable Isotope Analysis

Frozen tissue samples from each species-island combination served as the source for stable isotope data. Sample analysis followed previously established protocols (Post 2002, Michener and Lajtha 2007, Post et al. 2007) and was completed at the Boston University Stable Isotope Laboratory and the Scripps Institution of Oceanography Mass-Spectrometry Lab. In summary, frozen tissue samples were first freeze-dried for 24 hours to remove moisture and then ground to a fine powder using a mortar and pestle or mechanical grinder mill (Wig-L-Bug®). A 1.0-1.25 mg sample of powdered tissue was weighed out (to nearest 0.01 mg) in a tinfoil cup using a precision microelectric balance and subsequently encapsulated in their respective tinfoil cup. Individual samples were then flash combusted at 1800ºC in a Eurovector Carbon and Nitrogen elemental analyzer and the combustion products (CO_2, N_2 and H_2O) were separated chromatographically and introduced into GVI IsoPrime isotope ratio mass spectrometer, with

water removed using a magnesium perchlorate water trap. Stable isotope ratios of nitrogen (^{15}N to ^{14}N) and carbon (^{13}C to ^{12}C) were expressed as the relative per mil (‰) difference between the samples and international standards (Vienna PDB carbonate and N_2 in air, respectively). Values were reported in δ notation where $\delta^{15}N$ or $\delta^{13}C$ ratios were expressed by the equation:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = \left[\frac{R_{sample}}{R_{stondard}} - 1\right] \times 1000,$$

where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. To increase sample accuracy, one replicate per 10 samples as well as any initial anomalous results were rerun. To ensure consistent combustion among sample replicates, a known standard (e.g. peptone, a hydrolyzed animal protein from Sigma Chemical Company, glycine, or citrus leaves, SRM 1572) was run every 15 consecutive samples. If the known standard yielded results 0.15 ‰ above or below the documented standard value, the samples preceding the standard were rerun.

The dominant marine macroalgae in the central Pacific, *Halimeda* spp., was collected and processed for isotopic analysis to complement the examination of dietary consistency across islands. *Halimeda* spp. samples were collected from each island or atoll in the vicinity of the fish collection sites and brought back to the research vessel to be dried and stored individually in labeled sample bags. To prepare samples for stable isotope analysis, a small segment (~1.0 g) of each sample was cut near the tip of new growth. A total of 20 individual segments were collected from each island. For analysis, *Halimeda* spp. samples were placed in pre-labeled cleaned (acid washed using 5% HCl) 15 ml falcon tubes. Samples were then de-calcified by adding ~5 ml of 5% HCl to each falcon tube. After 24 hours the HCl solution was decanted and an additional 5 ml of 5% HCl was added to each falcon tube to ensure de-calcification of samples had taken place. The HCl solution was again decanted and samples were rinsed by adding ~10 ml of DI

water to each falcon tube, which was then capped, and gently shaken. The DI water was decanted and the process was repeated 3 times to ensure most of the HCl solution had been removed. Samples were then placed on labeled clean (combusted at 450°C for 12 hours) aluminum weigh boats and placed in drying oven at 60°C for 72 hours. Samples were then removed from the drying oven and ground to a fine powder using a mechanical grinder mill (Wig-L-Bug®). A 1.4-1.6 mg sample of powdered *Halimeda* spp. was weighed out (to nearest 0.01 mg) in a tinfoil cup using a precision microelectric balance and subsequently encapsulated in their respective tinfoil cup. Individual samples were then processed through a mass spectrometer as outlined above to obtain stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$).

References

Altabet MA (2001) Nitrogen isotopic evidence for micronutrient control of fractional NO utilization in the. Limnol Oceanogr 46:368-380

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007-1012

Bush GW (2009) Establishment of the Pacific Remote Islands Marine National Monument: a proclamation by the President of the United States of America. , vol. 8336. Federal Register, Washington, DC, pp 1565-1575

DeMartini EE, Friedlander AM, Sandin SA, Sala E (2008) Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. Mar Ecol-Prog Ser 365:199-215. doi: Doi 10.3354/Meps07501

Gove JM et al. (2016) Near-island biological hotspots in barren ocean basins. Nature Communications 7. doi: 10.1038/ncomms10581

Gove JM, Merrifield MA, Brainard RE (2006) Temporal variability of current-driven upwelling at Jarvis Island. Journal of Geophysical Research: Oceans (1978–2012) 111

Gove JM et al. (2013) Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. Plos One 8:e61974

Hyslop EJ (1980) Stomach Contents Analysis - a Review of Methods and Their Application. J Fish Biol 17:411-429

Maragos J et al. (2008) US coral reefs in the Line and Phoenix Islands, Central Pacific Ocean: Status, threats and significance. Coral Reefs of the USA:643-654

Michener RH, Lajtha K (2007) Stable isotopes in ecology and environmental science. Blackwell, Oxford

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179-189. doi: Doi 10.1007/S00442-006-0630-X

Randall JE (1967) Food habits of reef fishes of the West Indies. Studies in Tropical Oceanography 5:665-847

Sandin SA et al. (2008) Baselines and degradation of coral reefs in the northern Line Islands. Plos One 3:e1548. doi: ARTN e1548 DOI 10.1371/journal.pone.0001548

Sandin SA, Walsh SM, Jackson JBC (2010) Prey Release, Trophic Cascades, and Phase Shifts in Tropical Nearshore Ecosystems. Island Press, Washington, DC

Online Resource 2. Results of the systematic stomach analyses outlining the two-tiered hierarchal approach used to classify diet constituents for the Piscivore-invertivores. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Abbreviated fish species codes are as follows: LU.BOHA = *Lutjanus bohar*; CE.UROD = *Cephalopholis urodeta*; and PA.ARCA = *Paracirrhites arcatus.*

Diet category (coarse groups)	Diet category (subgroupings)	Example constituents	LU.BOHA	CE.UROD	PA.ARCA
Fishes			X	X	X
	Fishes	Labridae (*Pseudocheilinus* sp)		X	
		Pomacentridae (*Chromis* sp)		X	
		Gobiidae			X
Invertebrates			X	X	X
	Cephalopoda	octopi and squid	X	X	
	Other invertebrates			X	X
		Echinodermata (brittle stars, sea urchins)			X
		Gastropoda (snails)		X	X
		Unidentified invertebrate		X	X
Crustaceans			X	X	X
	Decapoda	crabs, megalopes, shrimp	X	X	X
	Stomatapoda	mantis shrimp		X	X
	Isopoda	isopods	X		
	Megalope	larval crustacean	X	X	

	Other crustaceans		X		X
		Amphopoda (amphipods)			X
		Copepoda (Calanoida, Poecilostomatoida, Cyclopoida, Harpacticoida)	X		X
		Unknown crustacean	X		
Other	Other	Calcifed algae (*Halimeda* sp)		X	X
		Early and Late algae	X	X	
		Other	X		

Online Resource 3. Results of the systematic stomach analyses outlining the two-tiered hierarchal approach used to classify diet constituents for the Planktivores. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Abbreviated fish species codes are as follows: PS.BART = *Pseudanthias bartlettorum;* and CH.MARG = *Chromis margaritifer.*

Diet category (coarse groups)	Diet category (subgroupings)	Example constituents	PS.BART	CH.MARG
Eggs			X	X
	Fish eggs		X	X
	Egg sacs		X	X
Larvacea	Larvaceans	tunicate, appendicularia	X	X
Foraminifera	Foraminifera	amoeboid protist	X	X
Other			X	X
	Gastropoda	Snail	X	
	Other		X	X
		Isopoda (isopod)		X
		Cladocera (water fleas)	X	
		Ostracoda (seed shrimp)	X	X
		Worm		X
		Trichodesium (cyanobacteria)	X	X

Clear case	X	X
Textured ball	X	X
Unidentifiable	X	X
Other	X	X

Online Resource 4. Results of the systematic stomach analyses outlining the two-tiered hierarchal approach used to classify diet constituents for the Grazer-detritivores. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Abbreviated fish species codes are as follows: AC.NIGR = *Acanthurus nigricans*; CT.MARG = *Ctenochaetus marginatus*; and ST.AURE = *Stegastes aureus.*

Diet category (coarse groups)	**Diet category (subgroupings)**	**Example constituents**	**AC.NIGR**	**CT.MARG**	**ST.AURE**
Invertebrates			X	X	X
	Foraminifera			X	X
	Other invertebrates	snails, bivalves	X	X	X
Early algae			X	X	X
	Filament	*Cladophora* sp., *Polysiphonia* sp., *Sphacelaria* sp.	X	X	X
	Cyanobacteria	*Moorea* sp., *Lyngbya* sp., *Schizothrix* sp.	X	X	X
	Net-like	*Microdictyon* sp., *Martensia* sp.	X	X	X
Late algae			X	X	X
	Complex cylinders	*Gelidium* sp., *Graciliaria* sp., *Laurencia* sp.	X	X	X
	Foliose	*Ulva* sp., *Dictyota* sp.	X	X	X
	Thick / leathery	*Sargassum* sp., *Turbinaria* sp.	X	X	X

Calcified algae			X	X	X
	Calcified algae	jointed calcareous (*Jania* sp., *Amphiroa* sp., *Halimeda* sp.) calcareous crust (*Peyssonellia* sp., Crustose Coralline Algae)	X	X	X
Sand	Sand		X	X	X
Other	Other		X	X	X

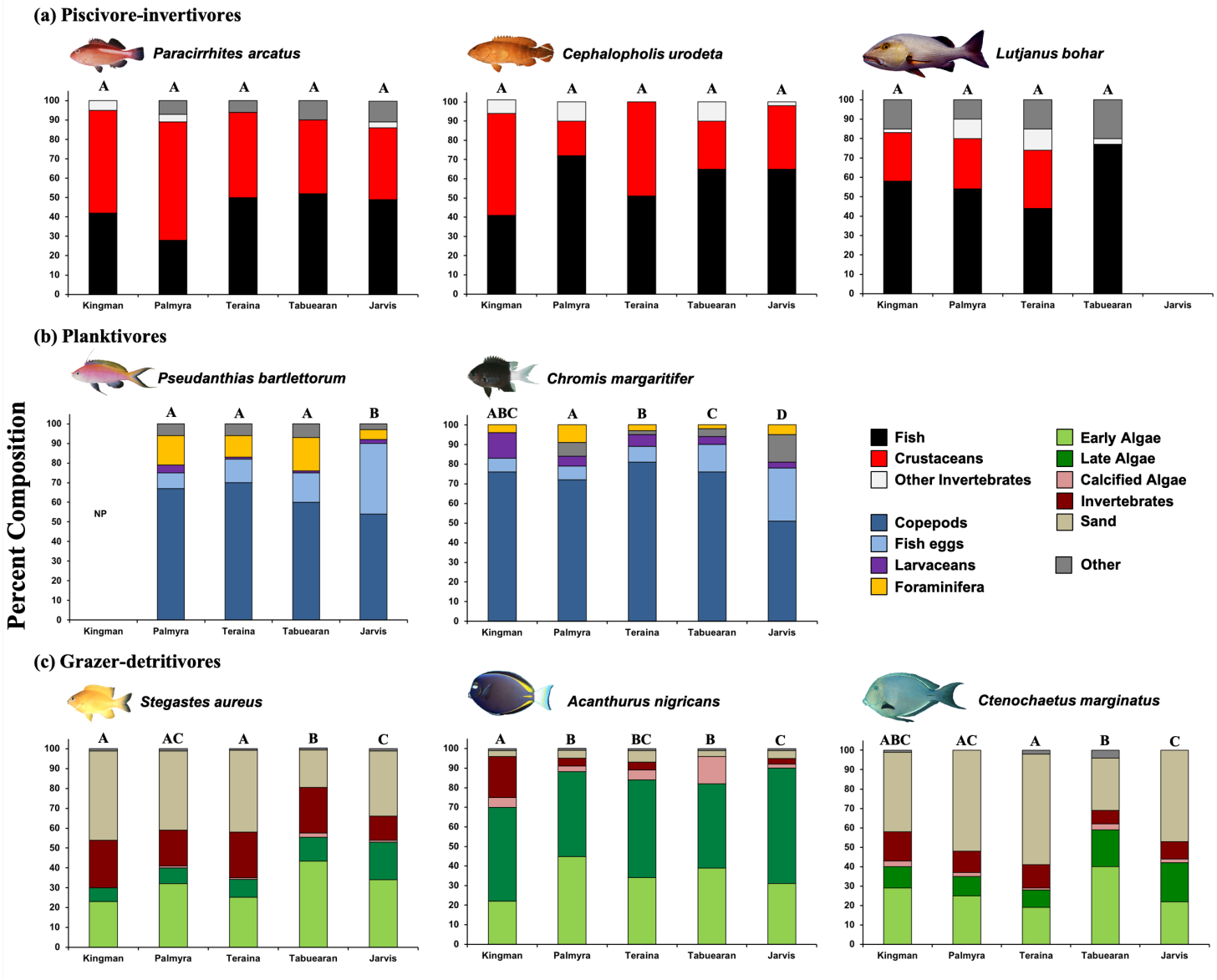
Online Resource 5. Results of the systematic stomach analyses for the piscivore-invertivores species across 5 survey islands identifying the mean size of prey (g) for each species and sample size given as number analyzed.

Species		**Kingman**	**Palmyra**	**Teraina**	**Tabuaeran**	**Jarvis**
Lutjanus bohar	Sample size	20	20	9	7	4
	Mean Prey Size (g)	4.16	13.29	13.11	1.78	
Cephalopholis urodeta	Sample Size	15	20	20	20	20
	Mean Prey Size (g)	0.55	0.59	0.37	2.29	0.54
Paracirrhites arcatus	Sample Size	20	20	20	20	20
	Mean Prey Size (g)	0.05	0.03	0.06	0.05	0.05

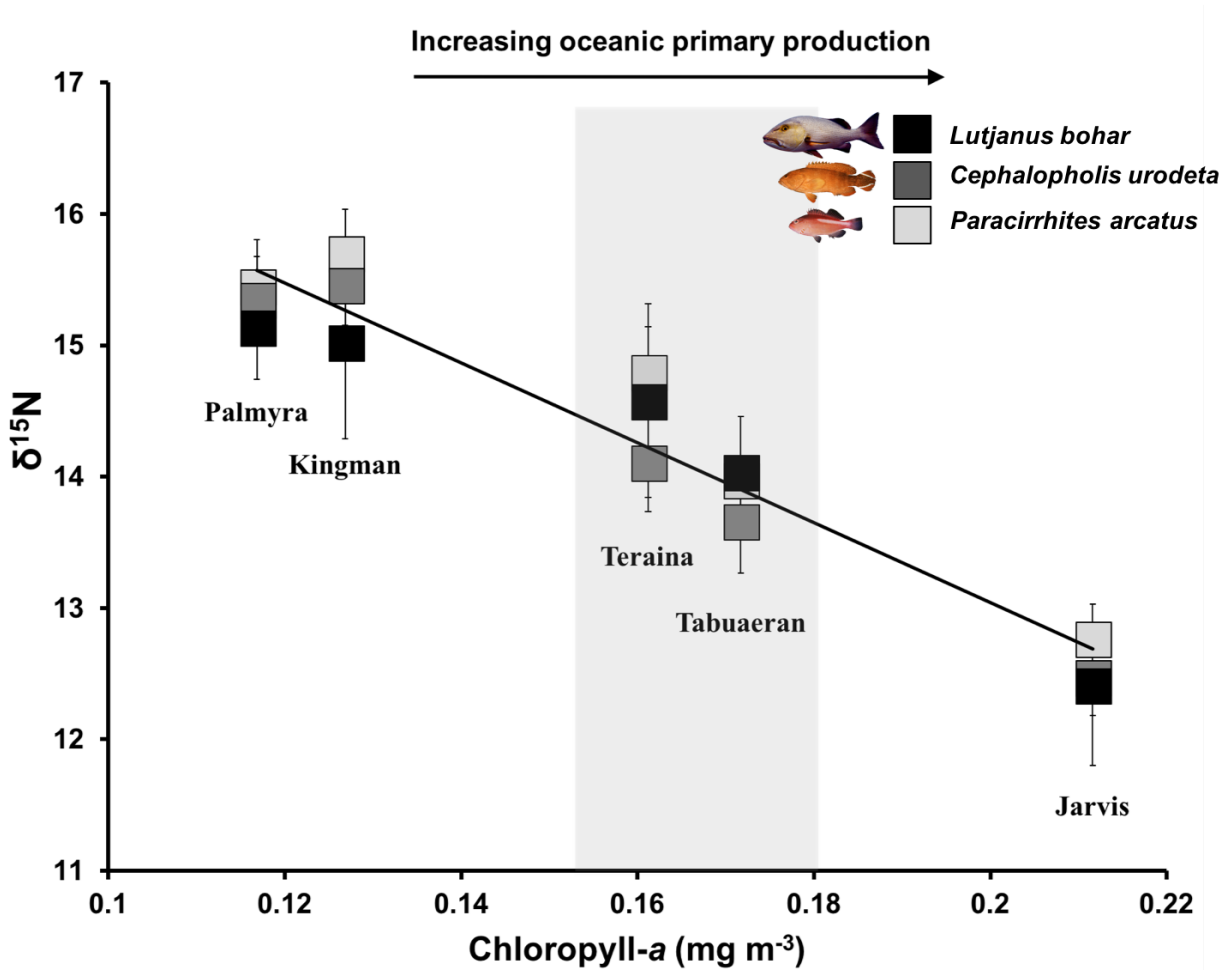
Online Resource 6. Output results of pairwise comparisons using a multinomial approach to examine stomach contents of eight species across the Northern Line Islands. Analysis was performed using the high-resolution dietary subgrouping data. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Significant difference based on $p \leq 0.01$. NP denotes that the species was not present at the island. Dashes indicate stomachs of sampled individuals were observed to be empty.

Functional Group **Species**	**Kingman**	**Palmyra**	**Teraina**	**Tabuaeran**	**Jarvis**
Piscivore-invertivores					
Lutjanus bohar	A	A	A	A	--
Cephalopholis urodeta	A	A	A	A	A
Paracirrhites arcatus	A	A	A	A	A
Planktivores					
Pseudanthias bartlettorum	NP	A	A	A, B	B
Chromis margaritifer	A, B	A	B	B	C
Grazer-detritivores					
Stegastes aureus	A	A, C	A	B	C
Acanthurus nigricans	A	B	C	D	E
Ctenochaetus marginatus	A, D	B	C	D	A,B,E

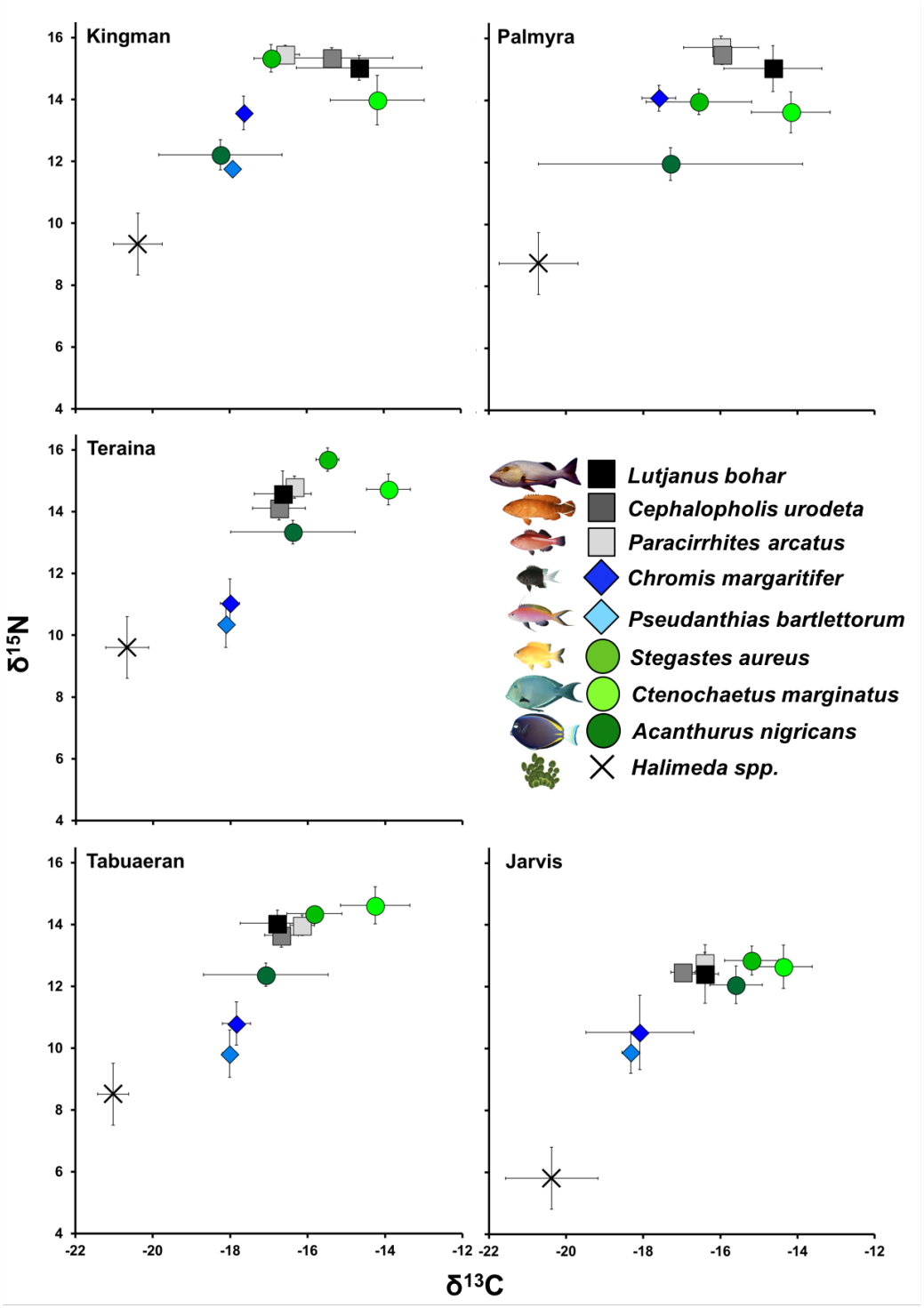
Online Resource 7. Percent composition of diet items observed in the stomachs of (a) the three piscivore-invertivores (*Lutjanus bohar, Cephalopholis urodeta, Paracirrhites arcatus*); (b) the two planktivores (*Pseudanthias bartlettorum* and *Chromis margaritifer*); and (c) the three grazers-detritivores (*Stegastes aureus, Acanthurus nigricans, Ctenochaetus marginatus*). Blanks indicate missing diet data for species-island combination and "NP" indicates species-island combination where species was not present at the island. At Jarvis, the sampled guts of *Lujtanus bohar* were observed to be empty. Letters above plots indicate results of multinomial pairwise comparisons.


(a) Piscivore-invertivores
Paracirrhites arcatus
Cephalopholis urodeta
Lutjanus bohar
(b) Planktivores
Pseudanthias bartlettorum
Chromis margaritifer
Percent Composition
NP
(c) Grazer-detritivores
Stegastes aureus
Acanthurus nigricans
Ctenochaetus marginatus
Kingman
Palmyra
Teraina
Tabuearan
Jarvis
Fish
Crustaceans
Other Invertebrates
Copepods
Fish eggs
Larvaceans
Foraminifera
Early Algae
Late Algae
Calcified Algae
Invertebrates
Sand
Other

Online Resource 8. Relationship between the mean $\delta^{15}N$ values (mean and ± 1 standard deviation) of three piscivore-invertivore fish species and estimates of nearshore primary production (mean chlorophyll-*a*) across the northern Line Islands. Solid line represents the fit from a least-squares linear regression ($R^2 = 0.97$, $P < 0.01$). Shaded area represents inhabited islands.



Online Resource 9. Description of stable isotope values ($\delta^{13}C$ - $\delta^{15}N$) for 8 species of coral reef fishes and the macroalgae (*Halimeda* spp.) plotted as bi-plots across the 6 northern Line Islands. All values are mean and ± 1 standard deviation.



Online Resource 10. Description of species-specific stable isotope values ($\delta^{13}C$ - $\delta^{15}N$) for eight species of coral reef fishes from the northern Line Islands. Symbols indicate island classifications (circles = remote islands; triangles = inhabited islands) and shading represents scale of oceanic primary production (lighter shading = less primary production). All values are means and ± 1 standard deviation.